A new species of arboreal viper (Serpentes: Viperidae: Atheris) from Cameroon, Africa

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Abstract.—A distinctive new species of the arboreal viper genus Atheris (A. broadleyi) is described from Cameroon, Africa. The new taxon inhabits moist evergreen and semideciduous transition forest in southern Cameroon, Congo, Central African Republic and Gabon. The new species previously has been confused with the widespread A. squamigera, but is distinguished from this species and other congeners by a combination of scale characteristics and a unique color pattern.

In a recent review, Broadley (1998) commented on an unusual color morph of Atheris squamigera from southern Cameroon. Perret & Mertens (1957) had previously mentioned the same population of Atheris from Moloundou in the extreme southeast of the country, and suggested that additional material was needed to ascertain this population's taxonomic status. Both of these descriptions agree with a series of Atheris I obtained during a herpetological survey of the proposed Lac Lobeké protected area of extreme southeastern Cameroon. Comparison of this material with museum specimens from Cameroon, Democratic Republic of the Congo, Central African Republic (CAR), topotypic A. anisolepis Mocquard (1887) and the holotype of A. squamigera (Hallowell, 1856) reveals that the southern, inland Cameroon population is distinct from all other Atheris species.

Methods

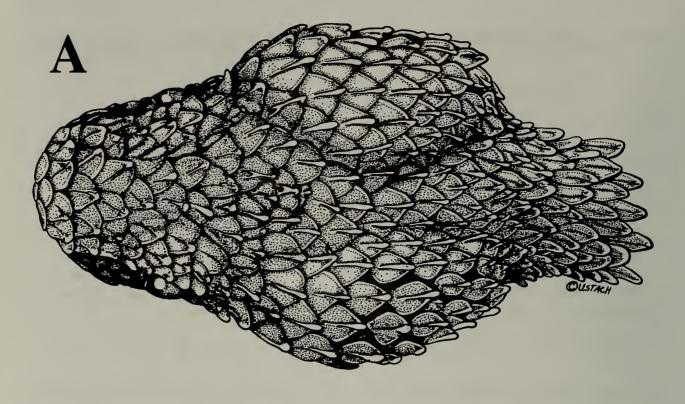
Specimens of the new *Atheris* were fixed in 3.7% formalin within 24 hr of collection. Specimens were transferred into 70% ethanol within two months after preservation.

Snout-vent length (SVL) and tail length (TL) were measured to the nearest mm us-

ing a meter stick. Other standard measurements were taken to the nearest 0.1 mm using dial calipers held under a dissecting microscope. Features of scalation were examined by holding preserved specimens under a dissecting microscope. Scale tergenerally follows Klauber minology (1956). Suprarostrals and interorbitals are used in keeping with Broadley (1998) for other members of the genus. Interrictal counts refer to scales across the back of the head between the posterior supralabials. Anterior body dorsal scale row counts were made approximately one head-length posterior to the head. Posterior body dorsal scale row counts were made approximately one head-length anterior to the vent. Color descriptions in preservative and life are based on a published standard (Smithe 1975). Institutional abbreviations refer to Academy of Natural Sciences of Philadelphia (ANSP), American Museum of Natural History (AMNH), University of Texas at Arlington Live Collection (DPL), University of Texas at Arlington Collection of Vertebrates (UTA). A list of specimens examined is given in the Appendix.

Systematic Account

During the summer of 1994 I made herpetological collections at various proposed



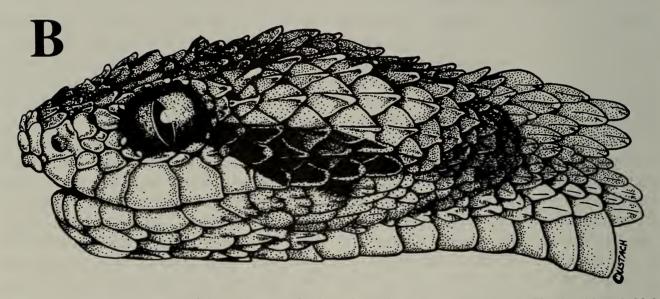


Fig. 1. (A) Dorsal and, (B) left lateral aspect of *Atheris broadleyi* holotype, UTA R-37801, head length 29.0 mm.

and existing protected areas throughout Cameroon. Specimens of *Atheris* taken at Lac Lobeké confirm long-standing impressions that this population is distinct. I propose that this new snake be known as

Atheris broadleyi, new species Figs. 1–2 and 5 (A)

Atheris squamigera squamigera.—Perret & Mertens, 1957:597

Atheris squamigera ssp. Perret, 1961:137 Atheris squamigera.—Broadley, 1998: fig. 8

Holotype.—University of Texas at Arlington Collection of Vertebrates (UTA) R-37801, mature female collected vicinity Lipondji village, East Province, Cameroon (2°23′05″N, 15°25′41″E), 1 Jun 1994 by D. P. Lawson (original field number DPL 3608).



Fig. 2. Atheris broadleyi, adult male from the type-locality, ca. 525 mm SVL, DPL 3646. Photo by D. P. Lawson.

Paratypes.—UTA R-37798-37800 and 44911-21, 10 adult and 4 juvenile females from the type-locality, collected between May and December 1994, UTA R-44957, an adult female collected in the vicinity Mbanjani village, East Province, Cameroon (ca. 5 road km south of the type-locality), 7 Sep 1997, and ANSP 20334, an adult male from Nola, Central African Republic (3°32′22″N, 16°02′51″E), collected 27 Oct 1934 by J. A. G. Rehn of the G. Vanderbilt Africa Expedition.

Definition and diagnosis.—A species of Atheris distinguished from all other members of the genus by the following combi-

nation of characters: lateral scales without serrated keel; supralabials in contact with suboculars (not separated by one or more scale rows); 14–18 interrictals; interorbitals keeled; rostral 3.5 to 4 times broader than high; scales in loreal region smooth or with only slight keel or knob; a dark postocular stripe persisting in adults; maximum total length of 765 mm or more; and a dark tail tip in adult females.

Specifically, Atheris broadleyi appears to be most similar to A. squamigera, but differs consistently by the combination of: a distinctive and consistent dorsal color pattern of citrine to greenish olive; checked

black, white and sky blue venter, and a dark postocular stripe; more oculars (mode of 15 versus modes of 12–14, see Table 1); and, greater length of 765 mm or more (versus 650 mm maximum for Cameroon A. squamigera). Additionally, A. broadleyi usually has more ventrals (mean of 162 ± 3.3 versus 157 ± 3.6) and fewer subcaudals (mean of 51 ± 4.9 versus 52 ± 3.2), and more infralabials (mode of 11 versus 10) than A. squamigera.

Atheris broadleyi lacks serrated keels on its lateral scales differentiating it from an East African group comprised of A. ceratophora, A. desaixi, A. katagensis, A. nitschei, and A. rungweensis with pronounced serrations on the lateral scales. Elongate supraocular scales forming a horn-like projection over the eye further distinguish Atheris ceratophora. Similarly, Atheris broadleyi lacks lanceolate or acuminate dorsal scales and fused lateral scale rows, differentiating it from the distinctive East African A. hispida and A. acuminata. Atheris broadlevi is distinguished from A. chlorechis by having fewer interrictals (14-18 versus 23 or more) and fewer mid-body dorsal scale rows (17-23 versus 25-36). In addition to differences in color pattern, Atheris broadleyi is distinguished from A. anisolepis by having completely keeled interorbitals (smooth in A. anisolepis), supralabials in contact with oculars (separated by a scale row in A. anisolepis), and usually fewer suprarostrals.

Description of holotype.—Rostral flattened, dorsal margin slightly concave medially, 3.5 times broader than high, contacting anteriormost supralabials, three unkeeled suprarostrals and divided left nasal; medial suprarostral the smallest, 1.3 times wider than high, right and left suprarostrals as wide as high; right and left nasals partially divided above the nares, left nasal further divided at anteriormost edge forming a separate small scale; nares large, covering approximately 30% of nasal, directed laterally and slightly posteriorly; internasals 5, strongly keeled, medial scale lying directly

above medial suprarostral but not separating two innermost internasals; interrictals 17; interorbitals 6, strongly keeled, those not contacting oculars enlarged and irregularly shaped; oculars 15/13, supra- and postoculars keeled, terminating in blunt knobs, suboculars and ventralmost preocular dorsoventrally compressed, knobbed but not keeled, two dorsalmost preoculars feebly knobbed, enlarged, extending anteriorly into loreal region; oculars separated from nasals by 6/5 smooth or feebly knobbed scales loosely arranged in three rows of 1/ 1, 1/2, 4/2; supralabials 11/10, 3-5 contacting suboculars; infralabials 11/11, 5-10 on each side feebly keeled, anteriormost in contact at the midline, separating mental from 5 pairs of chin shields; mental 2.3 times wider than deep; gulars strongly keeled; ventrals 159; subcaudals 50, entire; anal entire; dorsal scales about twice as long as wide, becoming shorter posteriorly, in 19-21-16 rows; keel on dorsals increasing in height from base, declining rapidly at apex, ending in slight knob; paraventrals larger than other dorsals, keeled, angled slightly ventrally.

Measurements (mm): SVL 550; tail length 110; eye diameter 5.1; head length 29; head width 21.2; distance from anterior margin of eye to nares 4.7 mm, to tip of snout 6.8 mm.

Color in preservative (ethanol after formalin) has not changed appreciably from life: dorsum of head uniformly citrine with olive-yellow keels; sides of head spectrum yellow extending onto lateral aspect of neck; face straw yellow; a diffuse dark stripe extending from the ventral posterior margin of the eye caudad to the rictus, incorporating the last three supralabials and posterior margin of the eighth, barely extending onto the last three infralabials; dorsum of body citrine anteriorly becoming greenish olive posteriorly, broken by 29 black-bordered sulphur yellow crossbands, crossbands on anterior half of body do not meet on midline, becoming indistinct on neck, posterior 15 crossbands conspicuous,

complete across the dorsum; tail with 9 moderately distinct, complete crossbands; tail tip black; interstitial skin color varied, corresponds to dorsal color pattern; throat and neck white; venter sky blue, irregularly suffused with white anteriorly, becoming increasingly darker posteriorly; white blotch on lateral portion of every third and/or fourth (occasionally second) ventral scale extending onto paraventral, blotches become more pronounced as venter darkens posteriorly, forming a checkered pattern; ventral color extends onto paraventrals and occasionally onto adjacent dorsal scale.

Variation.—The 15 paratypes closely resemble the holotype in color, pattern, and scalation. Posterior portions of the venter in some individuals (including the only male in the type series) are more uniformly dark than that of the holotype, but always have distinct white lateral blotches. Specimens from the western extent of the range (see below) may be less boldly patterned, and are almost uniformly citrine/greenish olive with barely discernable crossbands and postocular stripe (DPL 5508). Juveniles less than 300 mm SVL (UTA R-37798, 44913, 44918, 44920) have white tail tips, and remnants of a pale tail tip are present in two subadult specimens (UTA R-44915 and 44919). UTA R-37799 is the largest of the series (768 mm total length), UTA R-37798 the smallest (247 mm total length). One to three isolated scales are present in the interoculabial region in five of the paratypes, but do not completely separate oculars and supralabials. Scales in the loreal region are smooth in eight specimens and feebly knobbed in seven.

The paratypes exhibit the following variation (means and standard deviations in parentheses, modes in brackets, see Table 1): ventrals 157–169 (162 \pm 3.3); subcaudals 45–59 [50]; midbody dorsal scale rows 17–23 (20 \pm 1.6); anterior body dorsal scale rows 16–21 [19]; posterior body dorsal scale rows 13–18 [16]; ratio rostral width to height 3.2–5 (3.9 \pm 0.5); ratio medial suprarostral width to height 1–2.2 (1.2 \pm

0.3); ratio right suprarostral width to height 0.65–1.3 (0.91 \pm 0.2); suprarostrals 3–7 [3]; internasals 3–5 [5]; interorbitals 3–8 [6]; oculars 12–16 [15]; total scales in loreal region 3–7 (5.3 \pm 1.2) [6]; supralabials 9–12 [10]; infralabials 9–12 [11]; ratio of mental width to depth 1.3–2.5 (2 \pm 0.3); chin shields 4–7 [5]; interrictals 14–18 [17]; ratio eye diameter to head length 0.15–0.24 (0.18 \pm 0.02); ratio head length to SVL 0.05–0.07 (0.06 \pm 0.01); ratio head width to head length 0.64–0.84 (0.78 \pm 0.05); ratio eye-nares to head length 0.13–0.16 (0.15 \pm 0.01); ratio eye-snout to head length 0.21–0.27 (0.24 \pm 0.01).

Distribution.—Atheris broadleyi known from southern Cameroon from the Nyong River just southeast of Yaounde (11°11′12″E, 3°27′38″N, DPL 5508), south through the Dja Forest Reserve (Broadley 1998) and east at least as far as the Sangha region of the Central African Republic (Fig. 3). This distribution corresponds to a region previously mapped for Cameroon as moist evergreen and semideciduous forest (transition forest) comprised of Baillonella toxisperma and Gilbertiodendron dewevrei (CENADEFOR 1985). This region also features palm swamps and large scrub grassland clearings associated with seasonal high water tables (D. Thomas, pers. comm.). The distribution of Atheris broadleyi presumably follows this forest type into northern Gabon and Congo.

Atheris broadleyi was the most common snake in the Lac Lobeké, Cameroon survey, but does not appear in a slightly larger collection from the vicinity of Oesso, Congo, just across the Sangha River (Kate Jackson, pers. comm.). Atheris broadleyi is abundant near the type-locality. Local collectors obtained 24 specimens in 48 hours, indicating remarkable densities for a snake by Central African forest standards.

Etymology.—The specific epithet is a patronym for Donald G. Broadley in recognition of his considerable contributions to the herpetology of Africa in general, and

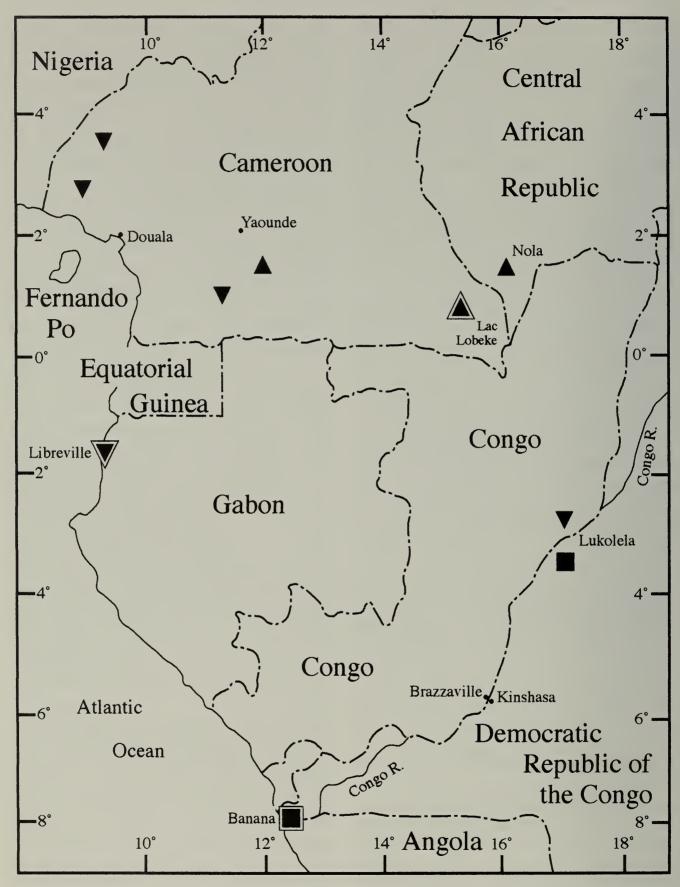


Fig. 3. Localities of *Atheris broadleyi* (triangles), *A. squamigera* (inverted triangles), and *A. anisolepis* (squares) in west Central Africa. Outlined symbols indicate type-localities.

his recent clarifications of the genus *Atheris* in particular.

Comparisons.—Broadley (1998) provided a key to the species of Atheris by which A. broadleyi is readily diagnosed from all members of the genus except A. anisolepis and the widely distributed and highly variable A. squamigera. Atheris broadleyi is also distinctly allopatric from all but A. squamigera. Although recognized in recent treatments (e.g., McDairmid et al. 1999, Broadley 1998, Trape & Roux-Estève 1995), A. anisolepis is similar to A. squamigera and its validity remains uncertain (Broadley 1998). Descriptive statistics and differences among A. broadleyi, A. anisolepis and A. squamigera are summarized in Table 1. For the purpose of comparisons with the new taxon, information for four populations of A. squamigera is presented separately in Table 1. Atheris squamigera is widely distributed in forests from Senegal to western Kenya (Spawls and Branch 1995). As evidenced by this species description and the intraspecific variability of A. squamigera (Table 1), previous descriptions of this taxon may have inadvertently increased the reported variation in many characters by combining distinct species with A. squamigera.

With the exception of occasional specimens which uniformly darken in preservative over time, color and pattern features of Atheris in preservative closely resemble those in life (pers. obs.). Atheris squamigera are most often apple green to turquoise blue with yellow crossbands above and yellow, green or blue ventrally (Fig. 4, Schmidt 1923, pers. obs.). Occasional specimens of A. squamigera from the Cameroon-Nigeria frontier (UTA R-44963, 44926, Stuck-Stirn 1979, Lawson 1993) and Congo (AMNH 45940, 51840), and specimens of A. anisolepis (AMNH 11898-99) are uniform spectrum yellow sparsely flecked with yellow-green spots. Atheris squamigera from the Congo River above Kinshasa (AMNH 45940, 45943, 45945, 51840) may be uniform yellow, turquoise

green, violet or a mottled combination of yellow and violet. Unlike *A. squamigera*, *A. broadleyi* appears to be highly consistent in color pattern.

South-central Cameroon is an area of possible sympatry between Atheris broadleyi and A. squamigera for which material is available. Specimens from Metet and Bitye (AMNH 5254, 51841-43) have a pronounced, dark postorbital stripe and several features of scutellation overlapping A. broadleyi. I have referred the south-central Cameroon material to Atheris squamigera on the basis of dorsal color pattern and scutellation. However, this area lies at the transition between the coastal moist evergreen forest of A. squamigera and the inland transition forest of A. broadleyi, and may represent an integration zone between the taxa (Fig. 3). Collections from other areas of possible sympatry at the southern limit of A. broadleyi are lacking.

In addition to differences in color and scalation, Atheris broadleyi differs from Cameroon A. squamigera in behavior and reproduction. Both in the field and in captivity, A. broadleyi are more aggressive, active and alert than A. squamigera, striking readily and repeatedly with little provocation (pers. obs.). Neonate Atheris broadleyi (Fig. 5 A) resemble the adults in coloration, but have a pale colored tail tip that disappears as they mature. This is in contrast to A. squamigera from western Cameroon that produce almost uniform charcoal-black offspring with pale green eyes and a pale tail tip (Fig. 5 B). These neonates attain the apple green or turquoise blue adult coloration with successive post-natal sheds. The pale tail tip persists in female A. squamigera from western Cameroon, but is lost in males from this population as they mature.

A pair of *Atheris broadleyi* collected as adults at the type-locality in 1994 and maintained in captivity in the United States have reproduced twice. Courtship and copulations were observed between 28 June and 11 July 1995, and 13 young (one deformed) were born on 10 February 1996. Courtship

Table 1.—Comparison of characteristics among Atheris broadleyi, A. anisolepis, and selected populations of A. squamigera. Mean values in parentheses, mode in

Characteristic	Atheris broadleyi $n = 16$	Atheris squamigera western Cameroon $n=13$	Atheris squamigera Kakamega Kenya $n = 5$	Atheris squamigera Congo $n = 4$	Atheris anisolepis $n=3$
Ventrals	157–169 (162)	149–163 (157)	153–160 (156)	152–156 (154)	150–162
Subcaudals	45–61 (51)	50-60 (55)	50–57 (53)	57–63 (59)	46-55*
Maximum total length in mm	768	629	738	403	*650
Supralabials	9–12 [10]	8-11 [10]	8–11 [10]	9-11 [9]	9–13
Infralabials	9–12 [11]	8–12 [10]	10-12 [10]	9–10 [10]	10-14*
Rostral width/rostral height	(3.9)	(4.3)	(3.7)	(4.1)	(3.2)
Suprarostrals	3-7, median never fused	3-7, median often fused	3	3–5	8-9
	to internasal	to internasal			
Interoculars	3–8 (5.8)	6-10 (6.8)	4-8 (6.2)	(9) 9	*8-9
Total oculars	12–16 [15]	11–16 [14]	13–15 [13]	12–15 [12]	12*-17*
Loreal scales	smooth	keeled	keeled	keeled	smooth
Adult female tail color	dark	white	white	NA	white?
Dorsal color pattern	Citrine to greenish olive	Green w/yellow cross-	Greeen w/yellow	Uniform green, yellow,	Uniform yellow or
	w/crossbands	bands or uniform yel-	crossbands	or mottled violet and	green
		low		yellow	
Postorbital stripe	present	usually absent	absent	absent	absent



Fig. 4. Atheris squamigera, adult male from vicinity Nguti, Southwest Province, Cameroon, ca. 375 mm SVL, DPL 5348. Photo by D. P. Lawson.

was observed on 13 July 1996, but no offspring were produced that year. Courtship was observed again on 10 June 1997 and continued for approximately one week. Five live and three stillborn young were produced on 17 February 1998. The male was observed courting and trying to copulate approximately one week prior to parturition. Specimens of A. squamigera from western Cameroon maintained under similar captive conditions to the A. broadleyi above have been observed in courtship in September-October and have given birth in April (pers. obs.). Pitman (1974) reported similar timing of reproduction for A. squamigera in Uganda.

Like its congeners, Atheris broadleyi is primarily nocturnal (Spawls and Branch 1995, pers. obs.). Specimens have been found as they were either active on the ground during or following evening rains,

or coiled among vine tangles, sitting in apparent ambush along arboreal rodent runways (pers. obs.). The few direct observations of this species in the wild occurred at the forest edge.

There is a preponderance of females in samples of both *Atheris broadleyi* and *A. squamigera* from Cameroon indicating a strong collecting bias or skewed sex ratio in the populations. Males of both species are considerably smaller than females. Males and females of *A. broadleyi* are much longer and more robust than their *A. squamigera* counterparts (Table 1, Figs. 2 and 4).

Acknowledgments

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Fig. 5. (A) Neonate *Atheris broadleyi* born to parents from the type-locality; (B) Neonate *A. squamigera* from wild-caught gravid female DPL 5318, Banyang-Mbo Wildlife Sanctuary, Southwest Province, Cameroon. Photos by J. A. Campbell.

drawing of the holotype, and M. Fost documented captive behavior and reproduction. I thank J. A. Powell and M. D. Powell for their friendship and logistic support in Cameroon, and P. Elkan and J. Ako for their help in the field. Field work was funded by the Wildlife Conservation Society through a grant from the U.S. Agency for International Development. Cameroon permits were issued by the Ministry of Environment and Forest. I also thank L. Ford (AMNH) and T. Daeschler (ANSP) for the loan of specimens examined in this study.

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Appendix Specimens Examined

Atheris anisolepis (3): Democratic Republic Of The Congo: Banana, Lower Congo; AMNH 11898–99. Kukolela, Congo R.; AMNH 45941.

Atheris broadleyi (5): Cameroon: East Province; DPL 3646, 3657, 5300, 5302. Center Province; DPL 5508.

Atheris squamigera (28): Cameroon: Bitye; AMNH 5254. Metet; AMNH 51841–43. Southwest Province; UTA R-31346, 44922–930, 44963, 45003–04. Democratic Republic Of The Congo: Lukolela, Congo R.; AMNH 45940, 45943, 45945, 51840. Gabon: ANSP 27253. Near the River Gaboon, Guinea; ANSP 6949 Holotype. Kenya: Kakamega; UTA R-12782, 13037, 19510, 26612, 32074.